Studies for Students.

COMPARATIVE STUDY OF PALÆONTOGENY AND PHYLOGENY.

CONTENTS.

INTRODUCTION.

PALÆONTOLOGY ought to be synonymous with phylogeny, and biology with ontogenetic study; but when most palæontologists are content to describe species from a few characteristics of adults, and to guess at their relationships and history, and when many zoölogists are satisfied with basing species on color or some other minor mark, while the life history of even most living forms is wholly unknown, the need of higher ideals is evident.

All modern classification is intended to be genetic and is based on comparison of a series of adults from successive ages of the earth, of which the present time is but an episode. Interesting and valuable investigations in phylogeny have been made in this way, but such genealogies cannot, as a matter of course, be more than approximate, for the geologic record itself is incomplete, and the life record still more fragmentary. We

have nowhere a uniform succession of rocks, and nowhere an unbroken genetic series. It has been shown how often the facies of the Pacific coast[1] region has changed, and how it now belonged to one faunal region, and now to another, each great change in faunal geography showing some physiographic revolution here or elsewhere. Thus the local series is broken and filled in from other regions, species being classed together because of resemblance, while their real relationship is unknown.

LAW OF ACCELERATION OF DEVELOPMENT.

Since the geologic record is so badly broken, and since modern faunas and floras are but the topmost branches of a tree whose stock is only partly known, naturalists were merely groping in the dark in their efforts to get a genetic classification. There was however a glimmer of light, although scarcely heeded. No one man seems to have been the discoverer of the law of acceleration of development, but like the idea of evolution, it was in the air, and disclosed itself in various ways to the prophetic vision of seekers after truth. J. F. Meckel,[2] a German naturalist, seems to have been the first to give scientific expression to the biogenetic law, in his formula, "Gleichung zwischen der Entwicklung des Embryo und der Thierreihe," *comparison of development of the embryo with the race of animals.* But Louis Agassiz, although not the discoverer, was undoubtedly the first to use the law as an aid in the systematic study of biology. While he regarded the various genera, not as ancestors and descendants, but as progressive steps in creation, still he saw the analogy between the stages of growth of the individual and these progressive steps. It was reserved for Alpheus Hyatt to formulate the law, and to strengthen theory with practical examples based on study of Cephalopoda.[3] In his later papers Professor

[1] JOUR. GEOL., Vol. III, May–June 1895, Mesozoic Changes in the Faunal Geography of California. J. P. SMITH.

[2] Syst. Vergl. Anat., I., Theil Halle, 1821.

[3] A. HYATT, Mem. Boston Soc. Nat. Hist., Vol. I, 1866–7, and Proc. Boston Soc. Nat. Hist., Vol. I, 1866, "Parallelisms of Individual and Order among the Tetrabranchiate Mollusks."

Hyatt has given a more exact and comprehensive definition of the law of acceleration or *tachygenesis:* "All modifications and variations in progressive series tend to appear first in the adolescent or adult stages of growth, and then to be inherited in successive descendants at earlier and earlier stages according to the law of acceleration, until they either become embryonic, or are crowded out of the organization, and replaced in the development by characteristics of later origin."[1] A still more definite statement by the same author is the following: "The sub-stages of development in ontogeny are the bearers of distal ancestral characters in inverse proportion and of proximal ancestral characters in direct proportion to their removal in time and position from the protoconch or last embryonic stage."[2] Since Hyatt's first paper the law has been rediscovered and renamed by Haeckel,[3] "das biogenetische Grundgesetz" and by Würtenberger.[4] But these naturalists, instead of adding anything to Hyatt's definition, have failed to reach its clearness and simplicity. The only real addition that has been made is Cope's[5] idea of retardation, by which is explained the separation in the ontogeny of the descendant of characters that occurred simultaneously in the ancestor. Cope says: "The *acceleration* in the assumption of a character, progressing more rapidly than the same in another character, must soon produce, in a type whose stages were once the exact parallel of a permanent lower form, the condition of *inexact parallelism.* As all the more comprehensive groups present this relation to each other, we are compelled to believe that *acceleration* has been the principle of their successive evolution during the long ages of geologic time. Each type has, however, its day of supremacy and perfection of organism, and a retrogression in these respects has succeeded. This has no doubt followed

[1] A. HYATT, Smithsonian Contributions to Knowledge, No. 673, "Genesis of the Arietidæ," Preface, p. ix.

[2] Proc. Am. Phil. Soc., Vol. XXXII, No. 143, A. HYATT, "Phylogeny of an Acquired Characteristic," p. 405.

[3] "Morphologie der Organismen," Vol. II; and "Anthropogenie," 1874.

[4] Ausland, 1873, and "Studien über die Stammesgeschichte der Ammoniten," 1880.

[5] Origin of the Fittest.

a law the reverse of acceleration, which has been called *retardation.* By the increasing slowness of the growth of the individuals of a genus, and later and later assumption of the characters of the latter, they would be successively lost."[1]

By a proper application of the law of acceleration as defined by Hyatt, and modified by Cope, all the facts of biology may be explained; there is no such thing as "falsification of the record." But as yet the law has had no great effect in classification, for most palæontologists have not approached their work from the biologic side, and biologists have been equally neglectful of the results attained by palæontology. A distinguished zoölogist once said to the writer, on being shown an ontogenetic series of ammonites, and the conclusions reached, "It is all beautiful, but almost too good to be true." In palæontology it is especially true that a naturalist may be a specialist in the fauna of one age, and know little of that of another. Hence the animals of various periods have been classified according to varying standards, all artificial. The only cure for these discrepancies is study of ontogeny, and comparison of stages of growth of the individual with ancestral genera. This will also prevent the description of supposedly new genera and species based on immature specimens, as has so often been done. The writer remembers once collecting numerous *Ceratites* in the Karnic limestone of the California Trias, much to his astonishment, for they ought not to occur so high up. He afterwards found, however, that they were not adults, but adolescent ceratitic stages of *Arpadites;* a similar case was the finding in the same horizon a *Tirolites* above its proper range, but it turned out to be the young of a *Trachyceras* that persisted unusually long in the *Tirolites* stage. At that time there was nothing in the description of these genera or any of their species to guide one, and so their ontogeny had to be worked out independently. But there is nothing in the description of almost any fossil genera and species to prevent just such mistakes, and they are constantly being made.

By careful study of ontogeny in comparison with phylogeny

[1] Origin of the Fittest, p. 142.

the palæontologist can correlate correctly fossil beds where even all the genera and species are new; he can even prophesy concerning the occurrence of *unknown* genera in certain horizons when he finds their minute counterparts in youthful stages of later forms; in fact he could often furnish just as exact a description of the form as if he had the adult genus before him.

NOMENCLATURE OF STAGES OF GROWTH.

In order to correlate ontogenetic stages with the generic changes seen in the development of the race it is necessary to have an exact scientific nomenclature. The most satisfactory is that given by Professor Hyatt in "Phylogeny of an Acquired Characteristic."[1]

TABLE OF ONTOGENETIC STAGES.

Stages	Stages	Substages	Comparison with phylogeny	
Embryonic	(1) Embryonic	Protembryo Mesembryo Metembryo Neoembryo Typembryo Phylembryo	Phylembryonic	Epacme
Larval	(2) Nepionic	Ananepionic Metanepionic Paranepionic	Phylonepionic	
Adolescent	(3) Neanic	Ananeanic Metaneanic Paraneanic	Phyloneanic	
Adult	(4) Ephebic	Anephebic Metephebic Parephebic	Phylephebic	Acme
Senile	(5) Gerontic	Anagerontic Metagerontic Paragerontic	Phylogerontic	Parac-me

With the embryonic stage the palæontologist can do nothing, except the very last substage or phylembryo, when the *Mollusca*, *Brachiopoda* and other groups begin to secrete their shells; but all the later stages are easily accessible in well-preserved material.

[1] Proc. Am. Phil. Soc., Vol. XXXII, No. 143, pp. 391 and 397.

The best example of correlation of ontogenetic stages with phylogeny is the genealogy of *Medlicottia*, worked out by Karpinsky,[1] who has shown that the Carboniferous genus *Pronorites* goes through the following stages: latisellate protoconch, phylembryonic; with the second suture it reaches the *Anarcestes* stage, nepionic; about the end of the first revolution the *Ibergiceras* stage begins, paranepionic; second revolution shows the *Paraprolecanites* stage, neanic; on the third whorl begins the *Pronorites* stage, adult. Thus with regard to *Pronorites* the genus *Anarcestes* is phylonepionic, *Ibergiceras* is phyloparanepionic, *Paraprolecanites* is phyloneanic. In the same work Karpinsky has shown that *Medlicottia* is a direct descendant of *Pronorites* and in its development goes through all the stages of the ancestral genus and adds several more. The first revolution of *Medlicottia* could not be studied, but on the second revolution was seen the *Ibergiceras* stage, metanepionic; on the third whorl the *Paraprolecanites* stage, paranepionic; at the end of the third whorl the *Pronorites* stage, beginning of the neanic; on the fourth whorl the *Sicanites* stage, end of the neanic: on the the fifth whorl the *Promedlicottia* stage, anephebic; and lastly, at end of the fifth whorl, *Medlicottia*, adult in characteristics, though not yet in size.

PALÆONTOGENY.

Groups available.—Vertebrates are out of the question for this sort of work, being too highly accelerated in their development; the stages that might be useful in phylogeny are gone through before the animal is capable of being preserved as a fossil. In the *Cœlenterata* the relations between Cenozoic and Palæozoic forms are not understood, and the ontogeny of available forms does not show stages that are striking enough to tell much. In *Echinodermata* difficulty of preservation of fossil forms makes ontogenetic study almost impossible, and recent forms have been too little studied for any comparison of stages of growth with ancient genera to be possible.

[1] Mém. Acad. Impér. Sci., St. Pétersbourg, VII Ser., Tome XXXVII, No. 2. "Ammoneen der Artinsk-Stufe."

The available groups are the *Brachiopoda*, the *Mollusca*, and the *Crustacea*.

Brachiopoda.—The brachiopods have this decided advantage, that they can be hatched in marine laboratories, and the various stages studied from the egg up, as has been done by Brooks, Kovalevski, Lacaze-Duthiers, Morse and Shipley, with the genera *Cistella*, *Glottidia*, *Lacazella*, *Liothyrina*, and *Terebratulina*. But it was reserved for the palæontologists Beecher, J. M. Clarke, and Schuchert to correlate the ontogeny of living forms with ancestral genera and give a biogenetic classification of the *Brachiopoda*[1] based on ontogenetic study.

In living specimens the subdivisions of the embryonic stage, protembryo, mesembryo, neoembryo, and typembryo may easily be made out, but since these are shell-less the work of the palæontologist begins with the phylembryonic substage, when the shell gland secretes the protegulum. From this upwards the palæontologist works on equal terms with the zoölogist, for the succeeding stages are capable of preservation, and may be compared with ancestral genera. Thus even the phylembryonic stage, or protegulum, is represented by the Cambrian genus *Paterina*, the ancestral prototype of all *Brachiopoda*.

Beecher and Schuchert[2] have also demonstrated that the *Ancylobranchia* (Terebratuloids) all go through a primitive Centronelliform stage, and that the *Helicopegmata* (spire-bearers) do the same and are for a while genuine *Ancylobranchia*. Schuchert's classification of the *Brachiopoda*, published in Eastman's translation of Zittel's *Text-Book of Palæontology*, 1896, may be taken as strictly biogenetic so far as the data now at hand make such a thing possible. And this is the only group of which we have a biogenetic classification.

[1] For correlation of stages of growth with generic changes, and for the literature on ontogeny and phylogeny of *Brachiopoda*, see papers by Dr. C. E. Beecher, Amer. Jour. Sci., Vol. XLIV, Aug. 1892, "Development of Brachiopoda," Part 2.; and Trans. Connecticut Acad. Sci., Vol. IX, March 1893, "Revision of the Families of Loop-bearing Brachiopoda;" and "The Development of Terebratalia Obsoleta Dall."

[2] Proc. Biol. Soc. Washington, Vol. VIII, July 13, 1893, "Development of the Brachial Supports in Dielasma and Zygospira."

Crustacea.—The only *Crustacea* that are useful for the study of palæontogeny are the trilobites, and since they are all extinct without leaving any descendants, modern biology can give us little help. We are thus to a greater extent than with the *Brachiopoda* thrown entirely on the ontogeny of fossils, and in this case, too, the various stages must be worked out from separate individuals. Many naturalists, beginning with Barrande, have worked on the ontogeny of trilobites, have described various stages, sometimes as larvæ, sometimes as adult genera or species, but they met with seemingly insuperable difficulties in correlating these stages with the genealogy. Dr. C. E. Beecher, however, has overcome these difficulties, presenting his results in a recent paper on "The Larval Stages of Trilobites,"[1] in which he shows that all trilobites go through a phylembryonic stage, protaspis, homologous to the protonauplius of the higher *Crustacea.* While no known genera are exactly like the protaspis, still there are several that retain many of its features. After the protaspis stage the various groups of genera develop in different directions, but all go through larval stages analogous to generic changes in their group. The protaspis itself of the later groups becomes more complicated by acceleration of development, but always retains its essential features. By means of this study Dr. Beecher has been able to give the beginning of a truly genetic classification of trilobites.[2]

Mollusca.—Of the *Mollusca* only the *Pelecypoda* and the *Cephalopoda* are of use to the student of palæontogeny, for the *Gastropoda* have not been classified in a satisfactory manner, and the larval stages even of living forms not well studied.

Pelecypoda.—Almost all that has been done in comparing genera of *Pelecypoda* with stages of growth is the work of Dr. R. T. Jackson,[3] who has shown that they all go through a phylembryonic stage, prodissoconch, analogous to the protegulum of

[1] Amer. Geol., Vol. XVI, Sept. 1895.

[2] Amer. Jour. Sci., Feb. and March 1897, "Outline of a Natural Classification of Trilobites."

[3] Mem. Boston Soc. Nat. History, Vol. IV, No. 8, 1890, "Phylogeny of the Pelecypoda."

Brachiopoda, the protoconch of *Cephalopoda* and *Gastropoda*, and the protaspis of trilobites. The prodissoconch is a straight-hinged, two-muscled, toothless, smooth-shelled, bivalve stage, corresponding to the primitive group of *Pelecypoda*. Even the monomyarian *Ostrea* goes through this dimyarian stage. Professor W. H. Dall[1] has used this and other facts in the development of the pelecypods, giving the most satisfactory classification up to this time. But from the very nature of the case, when the ontogeny of few living and no fossil forms is known, an evolutionary classification of pelecypods is impossible.

Cephalopoda.—The living dibranchiate cephalopods, *Octopus*, *Loligo*, *Spirula*, *Argonauta* and other common forms, are incapable of preserving the larval stages as fossils. The only living tetrabranchiate genus, *Nautilus*, can have its larval stages preserved as fossils, but is one of the old unspecialized types, not having changed greatly since the first nautilian shell, and consequently having no striking changes in its ontogeny.

The animals that are capable of giving the best proof of evolution are the ammonites. These branched off from the nautiloids at the beginning of the Devonian, continued increasing, diverging, became highly specialized and accelerated until their final extinction at end of the Cretaceous. Each ammonite goes through a larval history that is long and varied in direct proportion to the length of time from its period back to the Lower Devonian. Thus the *Nautilinidæ* are the first of the new stock, and their ontogeny is comparatively simple, there being no great changes from the larval up to the adult stages. The higher Devonian and Carboniferous forms go through several generic changes before they become adults, and the Mesozoic genera have still longer larval and adolescent periods, that is, longer in the sense of more complicated.

From the work of L. von Buch, Quenstedt, and others of the older palæontologists the increasing variety of forms from the goniatites of the Palæozoic to the ammonites of the Mesozoic

[1] Pelecypoda, Text-book of Palæontology, K. A. von Zittel, Revised English Edition, Vol. I, Part 1. Macmillan & Co., 1896.

was known long ago; these naturalists knew, too, that ammonites went through a goniatite stage of growth, without connecting this with evolution. By using their work we can get a comprehensive view of the development of ammonoids from the most primitive goniatites to the most highly developed ammonites, and thus construct a tentative family tree.

The simple primitive forms of the Lower Devonian branch out by the end of that age into two distinct stocks, the *Prolecanitidæ* and the *Goniatitidæ*, mostly low whorled, involute, with simple sutures and little ornamentation. Before the end of the Carboniferous some genera have already become ammonitic in the digitation of their sutures, as *Popanoceras*, *Thalassoceras*, *Pronorites*, and some have taken on ammonitic ornamentation of the shell, while the sutures remain simple and entire, as *Gastrioceras*. None of these forms, however, are very evolute, and the whorls are mostly rather low. In the Permian *Pronorites* and its descendants *Sicanites* and *Medlicottia* play an important part, *Arcestidæ* are already become important members of the fauna, the *Tropitidæ* are just beginning, while the *Glyphioceratidæ* are dying out. Some few genera still persist in the goniatitic stage, but most of them became ammonitic before the Trias was well on.

In the Trias the important groups are *Arcestidæ*, *Pinacoceratidæ*, *Tropitidæ*, *Ceratitidæ*, with numerous others less important as members of the Triassic fauna, but of great interest as ancestors of many of the chief families of the Jura and Cretaceous. In the Jura these ammonites reached their acme, branching out into very many families and subfamilies, increasing usually in complexity of sutures and variety of ornamentation. In the Cretaceous they gradually declined, dropping off one at a time until all were gone. The total number of *Ammonoidea* now described reaches about 5000, of which only a few hundred belong to the Palæozoic goniatites, the others belonging to the ammonites of the Carboniferous, Permian, and Mesozoic. Later than this no ammonoids are known.

Only simple radicles or stocks persist, but from time to time

certain genera branch off from the main stock, become highly specialized, and often give rise to so-called abnormal[1] forms, such as *Hamites*, *Baculites*, *Crioceras*, *Scaphites*, phylogerontic or degenerate genera, which do not perpetuate their race. These do not form a natural group, but are themselves even in some cases polyphyletic, as shown by their ontogeny; so far as examined their larval stages all correspond to various normal genera.

Of course there were phylogerontic genera that were not abnormal in shape; thus *Clymenia* branched off in the Upper Devonian into a variety of species, and disappeared as suddenly; *Medlicottia* reached its culmination in the Permian, barely managed to live on until the Trias, and disappeared without posterity, while the main stock of unspecialized *Prolecanitidæ* endured as long as the race. The number of phylogerontic forms increases in the Mesozoic, showing a constantly increasing tendency to become abnormal, until before the end of the Cretaceous the entire race of ammonoids becomes phylogerontic, and dies out from sheer lack of plasticity to modify itself further with changing conditions.

Such a general view or family tree of the ammonoids may be seen in any of the text-books of palæontology, especially those of Steinmann,[2] and of K. von Zittel,[3] where we get the best attempts to represent our present knowledge and ideas of the genetic relationships of ammonites. These genealogies are, however, purely tentative, based not on ontogeny but on comparison of series of adults. This would undoubtedly be the safest way if we had a perfect series of genera and species, but such a thing is unknown, and can never be obtained, on account of the incompleteness of the geologic record, and the mixing of faunas by migration in the past.

The researches of Hyatt, Branco, and Karpinsky have given us a surer way; from their work we have learned that the *Ammonoidea* preserve in each individual a complete record of

[1] J. F. Pompeckj, Ueber Ammonoideen mit Anormaler Wohnkammer. Stuttgart, 1894.

[2] Elemente der Palæontologie. 1890. [3] Grundzüge der Palæontologie. 1895.

their larval and adolescent history, the protoconch and early chambers being enveloped and protected by later stages of the shell. And by breaking off the outer chambers the naturalist can in effect cause the shell to repeat its life history in inverse order, for each stage of growth represents some extinct ancestral genus. These genera appeared in the exact order of their minute imitations in the larval history of their descendants, and by a comparative study of larval stages with adult forms the naturalist finds the key to relationships, and is enabled to arrange genera in genetic series. They were all marine, never parasitic, and so with them there is no obscuring of the record; also in the *Mollusca* generic and specific characters show in the shell better than in the soft parts; so the classification of fossil ammonites is just as good as that of living shellfish.

Although genera appeared in the order of corresponding larval stages, they did not disappear in the same order; and so their survival under favorable conditions is liable to make confusion in the record, if one depends wholly on the study of series of adults. Such forms, for instance, as *Styrites*, *Tropiceltites*, *Miltites* and others that are now known only in the Karnic zone of the Upper Trias are undoubtedly such survivals, for they still have simple goniatitic sutures, very little ornamentation, and in general are more like Lower Triassic ammonites than members of the *Tropites subbullatus* fauna. The stray *Tirolites foliaceus*, which appears in the Alps and in California in this same fauna, is another survival of a Lower Triassic type, but fortunately we do know *Tirolites* in the horizon where it belongs. If this were not the case the naturalist would be very much puzzled at finding *Trachyceras* of the Karnic horizon going through a *Tirolites* stage in its early youth.

One great drawback to this work is that the ammonite faunas of the various ages have been classified by different specialists and on different principles, but all artificial. Thus the Triassic ammonites are divided into Leiostraca (smooth shelled), and Trachyostraca (rough shelled), a classification that cannot be extended even to Jurassic groups. The Trachyostraca are fur-

ther divided into *Tropitidæ*, with long body chamber, and *Ceratitidæ*, with short chamber. But neither of these groups is monophyletic, for it is quite probable, judging from their ontogeny, that members of both groups are derived from the *Goniatitidæ*, and others from the *Prolecanitidæ*. Further, the authorities agree in deriving the *Tropitidæ* from the *Glyphioceratidæ*, but the larval stages of some of the *Tropitidæ* show the undivided ventral lobe and an unmistakable resemblance to certain *Prolecanitidæ;* other so-called *Tropitidæ* show the divided ventral lobe at an early age, and a decided resemblance to the stock of *Glyphioceratidæ*.

In the same way most authorities agree that the Trachyostraca were all extinguished at end of the Trias, and that all the Jurassic and Cretaceous ammonites, with the exception of *Lytoceratidæ* and *Phylloceratidæ*, were derived from the radicle *Psiloceras*, and this, too, in spite of the fact that many of the genera are rough shelled, and in their larval stages show marked likeness to trachyostracan genera. Any naturalist can convince himself of this by looking at the young stages of Jurassic ammonites figured by Quenstedt.[1] Quite recently Professor W. Waagen[2] has called attention to the likeness of certain Trachyostraca to Jurassic genera, and indicated the probability of genetic relationships. But Mojsisovics[3] says that these similarities have nothing to do with relationship, but are purely "convergence phenomena," whatever that may mean. Resemblance of adults of Triassic and Jurassic forms might with some reason be ascribed to this mysterious agency, but surely no biologist would thus explain away the resemblance of larval and adolescent stages of Jurassic ammonites to adult Trachyostraca of the Trias. There was some excuse for such opinions as long as the fauna of the upper Trias was not well known, and there was apparently a great break in the series of ammonites. But after the appearance of the monographs of G. von Arthaber, Diener,

[1] Ammoniten des Schwäbischen Jura.

[2] Pal. Indica, Salt Range Fossils, Vol. II, p. 122.

[3] Das Gebirge um Hallstadt, Bd. II, p. 265.

Mojsisovics and Waagen,[1] on the Triassic faunas of the Alps, Himalayas, the Salt Range of India, and Siberia, there is no longer any such excuse. Ancestral types, long predicted by larval stages of Jurassic ammonites, may be seen in these works, as, for instance, *Tropiceltites*, which is exactly like the neanic stage of *Amaltheus;* but the great variety is confusing, and correlation difficult, on account of unsatisfactory classification.

The only solution of the problem is to classify genetically the Palæozoic goniatites, and from them work upwards into the Permian and Lower Triassic ammonites. These older groups have simpler larval stages, are not very greatly accelerated, and repeat clearly their ancestral history. When this is done the radicles will all be known, and when we know the stock of the tree, the branches that came off in the higher Trias, Jura, and Cretaceous will offer no difficulties. The most systematic attempt to do this is Haug's paper, "Les Ammonites du Permien et du Trias;"[2] but his classification is based wholly on the character of the sutures, and neglects other characters, such as sculpture and shape of the whorls. Thus Haug[3] places *Eutomoceras* with the prionidian family *Trachyceratidæ*, disregarding its ontogeny, which places it undoubtedly with the *Tropitidæ*. But no classification based entirely on one character can be truly genetic. Hyatt[4] in his monographs on the ontogeny of ammonites has shown us the way; Branco by his studies of the larval stages of ammonoids has accumulated a great mass of accurate data that can be used with confidence even by the student that rejects his theories as to classification. And Karpinsky, by using the methods and principles discovered by these naturalists, has worked out the genealogy of one of the chief stocks of the earlier ammonites.

[1] For the literature on Triassic faunas see JOUR. GEOL., Vol. IV, No. 4, J. P. SMITH, "Classification of Marine Trias."

[2] Bull. Soc. Géol. France, II Ser., Vol. XXII. 1894, No. 6.

[3] Op. cit., p. 408.

[4] Bull. Mus. Comp. Zoöl., Vol. III, No. 5, 1872; and Smithsonian Contrib. to Knowledge, "Genesis of the Arietidae," and other papers.

This way lies the truth, and not in groundless speculations such as many students of cephalopods are prone to indulge in.

Method of working.—In order to succeed, one must select material with great care, preferably limestone that is soft but not so weathered as to crumble, nor so brittle as to shatter. One's finger nail and some steel dental chisels are all the tools needed for breaking off the outer whorls of young ammonites. A microscope with thirty diameters magnifying power is the most satisfactory, although higher powers are occasionally needed. For studying surface markings a strong pocket lens is usually sufficient; the specimen should then be placed dry on white cardboard. For observing the sutures, or shape of the whorls, the specimen should be placed on cardboard in a drop of water, spread out so as not to distort the object. The water, being slightly viscous, will also hold the small object in any position. For taking measurements a micrometer eyepiece is needed, especially in drawing, for the *camera lucida* is not very satisfactory for drawing opaque objects. Sections can easily be cut by grinding with emery powder on a glass plate.

The accompanying illustrations will give an idea of how the facts are ascertained. A number of well-preserved adults of a species are selected, and the outer coils are pulled off piece at a time under water, until a complete series is obtained, representing every change in growth. All the pieces of whorls are preserved, but often it is possible to have a complete series in one specimen. The individuals representing stages of growth are kept separate, in small glass tubes attached to cards for labels, on which are noted the measurements of the specimen, stage of growth, and such other facts as are wanted for ready reference.

On plate *A* are shown the results of some work of this character. The species selected was *Schloenbachia* aff. *chicoensis* Trask, from the upper Horsetown beds, top of Lower Cretaceous, from Phœnix, Oregon. Fig. 1 shows the protoconch with part of the first whorl drawn as if unrolled. The protoconch is phylembryonic, representing the primitive ammonoid; the first suture, angustisellate, with narrow lateral lobes and saddles, is

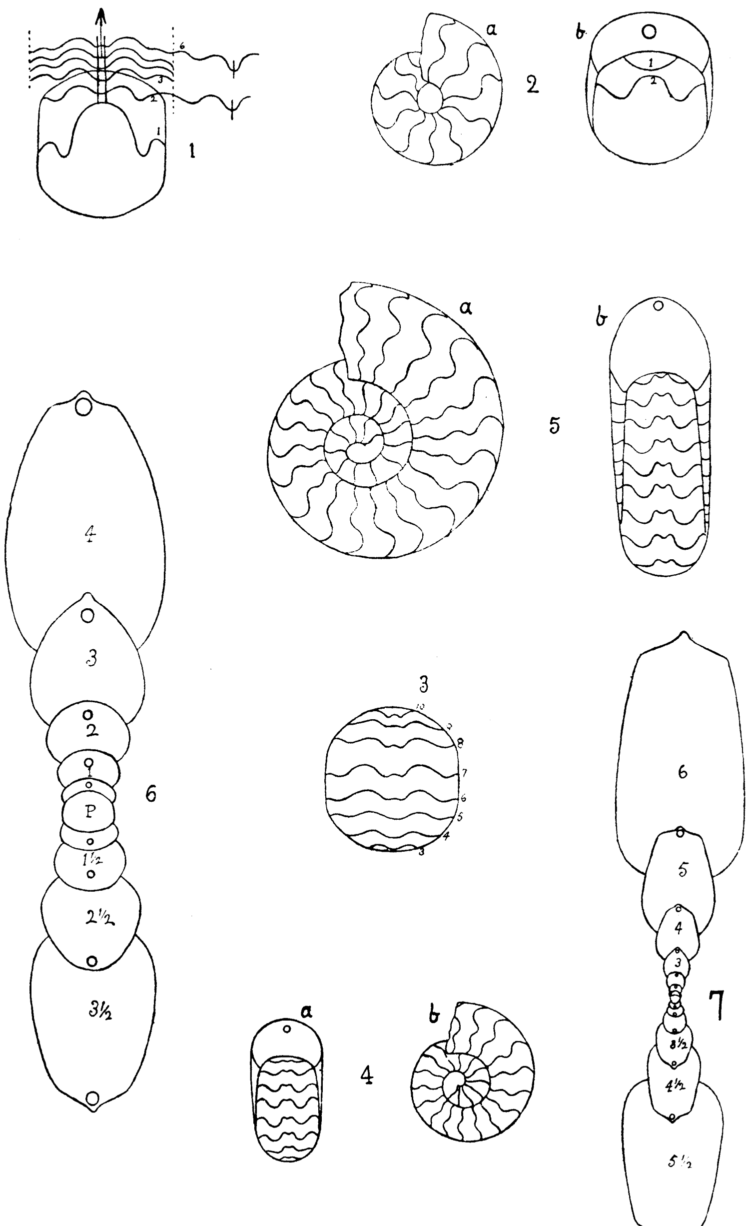

PLATE A.

ananepionic; the second suture with the abdominal lobe is metanepionic, and represents the ammonoid radicle *Anarcestes;* the third and fourth sutures correspond to *Tornoceras* and *Prionoceras;* the fifth suture is a transition from *Prionoceras* to *Glyphioceras;* and the sixth with the divided ventral lobe represents *Glyphioceras.*

Fig. 2 shows the larval stage, at diameter of $0^{mm}.68$, three-fourths of the first whorl. It has a low broad involute whorl, with divided ventral lobe, one lateral lobe, and another on the umbilical border. This stage is paranepionic, and is like the older species of *Glyphioceras.*

Fig. 3 shows the development of the sutures from the third to the tenth, on a specimen of diameter $0^{mm}.64$.

Fig. 4 shows the advanced *Glyphioceras* stage, with lobes and saddles, well developed, at diameter of $1^{mm}.20$; the second lateral lobe already begins to show on the umbilical shoulder. This stage is transitional to *Gastrioceras.*

Fig. 5 shows the end of the paranepionic stage, corresponding to *Paralegoceras*, at $2^{mm}.25$ diameter; the umbilicus widens, the whorls become higher and narrower, and a third lateral lobe appears on the umbilical border. The sutures still remain goniatitic, but in the next stage, ananeanic, ammonitic ornamentation, in the shape of a keel, appears at $2^{mm}.70$; and at $3^{mm}.20$ diameter the first lateral saddle becomes indented, and the adolescent stage is well along.

Fig. 6 shows a cross section through the center, diameter $6^{mm}.25$, four whorls, paraneanic. The inner whorls are low and broad, and the later ones become successively higher and narrower in proportion.

Fig. 7 shows a section through the protoconch, diameter $22^{mm}.25$, six whorls, adult stage; the relative increase of height of the whorls and the squaring of the abdominal shoulder is quite marked as the adult stage advances.

On these figures may be seen increase in number of lobes and saddles, change in position of the siphon from median to external, and the development of the whorls, in height, width, and involution.

By following this method on suitable material the complete ontogeny of any species may be worked out. In order to work out the phylogeny of any form it is necessary to combine this with comparative study of antecedent genera and species. When this is done for all the *Ammonoidea*, their genealogy will be more perfectly known than any other family tree possibly can be.

PLATE *A*.

FIG. 1. Protoconch of *Schloenbachia*, showing the first six sutures of the attached coil. Enlarged thirty times.

FIG. 2. Larval stage of *Schloenbachia*, diameter $0^{mm}.68$; thirty times enlarged; three-fourths of first whorl. *2a*, side view; *2b*, front view.

FIG. 3. Larval stage of *Schloenbachia*, diameter $0^{mm}.64$; thirty times enlarged. Showing sutures from the third to the tenth. From above.

FIG. 4. Larval stage of *Schloenbachia*, diameter $1^{mm}.20$; fifteen times enlarged. One and a half whorls. *4a*, front view; *4b*, side view.

FIG. 5. End of larval stage of *Schloenbachia*, diameter $2^{mm}.25$; fifteen times enlarged. *Paralegoceras* stage. *5a*, side view; *5b*, front view.

FIG. 6. Cross section of *Schloenbachia*, diameter $6^{mm}.25$; fifteen times enlarged; four whorls. Adolescent stage. The protoconch is seen in the center *P*.

FIG. 7. Cross section of *Schloenbachia*, $22^{mm}.25$; three and a half times enlarged; six whorls. Adult stage.

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